SEED REGENERATION IN LONG-UNBURNT AND RECENTLY-BURNT HEATHLAND AT WYPERFELD NATIONAL PARK

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Heathland quadrats were reassessed 14 years after the first data were collected. Vascular plant species richness increased at sites burnt in the interim, but also increased at sites unburnt in the intervening period. At the burnt sites, the species richness of all perennial growth forms increased (ie. serotinous shrubs, non-serotinous shrubs and perennial herbs), while richness of annual species declined. At the unburnt sites the increase in total species richness was solely due to an increase in the richness of non-serotinous shrubs. Many species of non-serotinous shrubs are not specifically adapted to exploiting post-fire regeneration opportunities, and here successfully regenerated by seed in the absence of fire. Post-fire development in heathland is not simply a gradual decrease in species richness as the vegetation ages. Species' proportions and composition change, depending on each site's unique characteristics.

Key words: heathland, seedling regeneration, fire, growth form.

PLANT species regeneration in heathland is usually assumed to be largely restricted to the period immediately post-fire, thus utilising the reported post-fire nutrient flush (O'Connell et al. 1978; Posamentier et al. 1981; Groves 1983; Rundel 1983; Bell et al. 1984; Wark et al. 1987; Handreck 1997). Most authors accept that the component species do not regenerate from seed in the absence of fire, although sporadic seed regeneration of a few species has been (exceptionally) reported (Frood 1979; Hnatiuk & Hopkins 1980; Bradstock & Myerscough 1988; Bradstock 1990; Enright et al. 1994). Species richness purportedly reaches a maximum shortly after fire and from there gradually declines as the heathland ages (McMahon 1977; Russell & Parsons 1978; Cheal et al. 1979; Groves & Specht 1981; Kruger 1983; Bell et al. 1984). In spite of these deaths, canopy gaps are not a characteristic of most older heathlands, due to increases in size of the long-lived dominants and scattered root-stock resprouting (Kruger 1983; Keeley 1986). Heathlands with canopy gaps deriving from death of dominants are very rare, as fires are usually frequent enough to prevent such maturation or 'senescence' (Hazard & Parsons 1977; McMahon 1977; Russell & Parsons 1978; Kruger 1983; Bradstock & O'Connell 1988; Hilbert and Larigauderie 1990).

An opportunity to test the ability of species to regenerate in the absence of fire and to test, or measure, species decline as heathland aged was presented by reassessment of heathland quadrats in Wyperfeld National Park. These quadrats were first assessed in 1978, as part of a preliminary study on the effects of fire in the Mallee National Parks of Victoria (Cheal et al. 1979).

The study site was in the sandplain heathlands of Wyperfeld National Park, in the Big Desert, Mallee region of north-western Victoria (Fig. 1). Wyperfeld is approximately 360 km north-west of Melbourne (466 km by road) and 330 km east–south-east of Adelaide (472 km by road). The main park entrance is at longitude 142°5′E and latitude 35°39′S.

Mean annual rainfall is 363 mm at Rainbow, with a weak winter maximum. The soils are highly podsolised, unconsolidated, quartzose sands.

Fig. 1. Location of Wyperfeld National Park.

The heathlands of the Big Desert are characterised by an open canopy (usually less than 40–50% projective canopy cover, *sensu* Walker & Tunstall 1981) rarely exceeding 1 m tall. The most common and consistent dominants are *Banksia ornata*[1], *Casuarina pusilla*[2], *Casuarina* sp. (=*Allocasuarina mackliniana sensu* Johnson 1982), *Leptospermum coriaceum* and *Leptospermum myrsinoides*. Smaller, lower-growing shrubs (in particular various heaths—*Acrotriche*, *Astroloma*, *Brachyloma* and *Leucopogon*, and small myrtles—*Baeckea*, *Calytrix*, *Kunzea pomifera* and *Micromyrtus ciliata*) are common, as are sedges and similar sclerophyllous monocotyledons. Grasses are rare, except for hummock-grasses (*Triodia* sp.) which may be locally common. Annuals are rare to absent, except after fires when they may be common for 1–2 years (after which they apparently disappear from the community, until the next fire). Ephemerals are uncommon, unlike in many other heathlands, with their substantial flora of orchids and lilies. Wyperfeld's heathlands are within Specht's 'Group B'—with *Lepidosperma* and *Cryptandra*, lacking *Actinostrobus*—'South Australia extending into the drier side of the Great Dividing Range in south-eastern Australia' Specht (1981: 266–269).

METHODS

Quadrats originally assessed as part of the earlier study by Cheal et al. (1979) were relocated in the field during 1992. All quadrats were 10 m × 10 m squares. Occasionally, the precise quadrat location could not be guaranteed, as the 1978 quadrats were only temporarily marked. Most markers were found again in 1992, although there was difficulty in relocating two of them. Quadrats that could not be reliably relocated were not included further. Nevertheless, most of the earlier quadrats were relocated, with each boundary being less than 1 m from its former location. These near-identical quadrats were reassessed in 1992 (14 years between assessments). On both occasions I assessed the 20 quadrats (thus differences cannot be attributed to operator effects). Thirteen of the quadrats had not been burnt between 1978 and 1992—the most recent fire in this part of Wyperfeld National Park was in 1959. The other seven quadrats were subject to wildfire in 1984—before that date there was no evidence of a previous fire, apart from map notes from a survey by Bolton (1915).

The quadrats were assessed in October 1978 and again in October 1992. All vascular plant species growing in, or projecting over, the quadrats were identified and assigned a cover-abundance value, based on a modified Braun–Blanquet Scale (as described in Cheal & Parkes 1989).

Results were compared using *t*-tests for paired samples. The two different sites (quadrat clusters, ie. long-unburnt and burnt in 1984), with their differing fire histories, were not compared with each other. The comparison is time-based, ie. the same quadrats in 1978 and again in 1992.

RESULTS

Although the 1978 quadrats and the 1992 quadrats were substantially coincident, a few may not have been perfectly so. All quadrats were considerably larger in area than the minimal area determined within these heathlands (Fig. 2).

The mean difference in total species number recorded in 1978 and that recorded in 1992 was an increase of 3.5 species. If the change in species number was merely some effect of slight spatial displacement in quadrat location and, at the same time, there had been no change in species packing in the vegetation over the intervening 14 years, then one could reasonably expect a decrease in species number as an increase. Yet 12 out of 13 unburnt quadrats recorded an increased species number in 1992 when compared with 1978—an unlikely event if change in species number was solely attributable to any slight variation in precise quadrat locality ($p = 0.003$—calculated from the binomial distribution; increase versus decrease in species number over time). Any small distance quadrat displacement had a trivial effect on species composition.

Long-unburnt quadrats

For 12 of the 13 unburnt quadrats there was an increased number of vascular plant species in 1992 when compared with the same quadrats in 1978. In spite of the absence of fire for the intervening 14 years, species not present in the quadrats in 1978 established and grew. These 'new'

[1]Vascular plant nomenclature follows Walsh & Entwisle (1994) for conifers and monocotyledons, and either Walsh & Entwisle (1996) or (1999) for dicotyledons, unless indicated otherwise.
[2]After Hwang (1992).

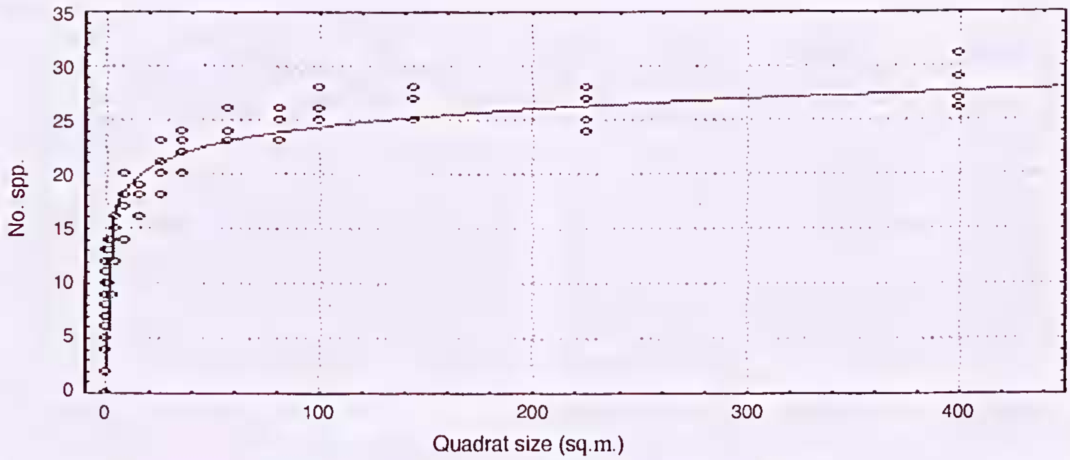

Fig. 2. Minimal area determination; Sandplain Heathland, Wyperfeld National Park.

(or 'newly recorded') species did not invade this vegetation community from outside. The species composition of quadrats within the one vegetation community is not homogeneous. Many species are scattered throughout the community and may not be present in all quadrats. Newly recorded species established from seed from nearby individuals, ie. from expected components of this heathland community, but formerly absent from this particular 10 m × 10 m sample.

This increase in species number is not due to an increase in the annuals nor the dominant serotinous shrubs (Table 1). The increase is principally due to the establishment and growth of a number of subordinate woody shrubs (both seed regenerators and root resprouters). These small shrubs all lack serotinous fruits, releasing their seed shortly after maturity.

Recently-burnt quadrats

Seven of the quadrats first assessed in 1978 had been burnt in the wildfire of 1984. The total species number, the number of serotinous shrub species, the number of non-serotinous shrub species and the number of herbaceous perennial species had all increased by 1992, whilst the number of annual species had decreased in the same interval (Table 2).

DISCUSSION

These data show that species richness was greater in 1992 than in 1978, for both long-unburnt and recently-burnt quadrats. This was expected for quadrats that had been burnt in the intervening 14 years, consistent with other studies (eg. Gill 1975; Russell & Parsons 1978; George et al. 1979; Gill & Groves 1981; Posamentier et al. 1981; Hobbs & Atkins 1990).

Recently-burnt quadrats

In the quadrats burnt in 1984 and hence sampled 8 years post-fire, the total number of species, number of serotinous species, number of perennial herb species (such as *Goodenia* spp., restiads, sedges and *Lomandra* spp.) and number of non-serotinous shrub species all increased after the fire. Presumably, removal of the formerly dense dominants (principally *Callitris* spp., *Kunzea pomifera*, *Leptospermum coriaceum* and *Triodia* sp.) enabled newly-regenerant plants to take advantage of the opportunities/niches thus offered. At the same time, the number of annual species in the vegetation was less in 1992 than in 1978. Before the 1984 fire there had been an extended period without fire (at least 69 years). The vegetation was dominated by non-serotinous woody species and included many annual species not normally constituents of heathland in Wyperfeld. The 1984 wildfire apparently led to an increase in serotinous shrubs and other woody species and a reduction, 6 years later, in the non-heathland, generalist, adventive annuals.

Long-unburnt quadrats

Some of the reassessed quadrats had not been burnt between the 1978 and the 1992 assessments.

Quadrat identifier[A]	Total spp. number[B] 1978	1992	Annual species 1978	1992	Serotinous shrubs 1978	1992	Perennial herbs 1978	1992	Non-serotinous shrubs 1978	1992	Dominance
A03056	19	25	1	0	1	2	10	10	7	12	Mixed
A03057	23	25	14	13	2	2	4	4	3	6	*Callitris*
A03058	21	27	3	4	1	0	8	13	7	9	Mixed
A03059	20	24	5	3	0	0	9	12	5	7	*Leptospermum*
A03062	25	30	1	2	2	2	12	14	10	12	Mixed
A03063	24	26	5	6	1	0	11	8	5	11	*Leptospermum*
A03064	26	23	1	3	1	0	15	10	9	9	*Leptospermum*
A03065	34	35	3	3	3	4	12	14	16	15	Mixed
A03066	30	31	3	2	4	4	11	12	12	13	Mixed
A03067	35	38	2	2	4	4	11	13	16	18	Mixed
A03106	28	33	10	11	1	1	4	10	12	10	*Callitris/ Leptospermum*
A03109	36	45	27	31	1	1	5	9	2	4	*Callitris*
No ID No.	27	32	16	15	0	0	5	8	4	6	*Leptospermum*

t-test results

	Total spp. number 1978	1992	Annual species 1978	1992	Serotinous shrubs 1978	1992	Perennial herbs 1978	1992	Non-serotinous shrubs 1978	1992
Mean	26.8	30.3	7.0	7.3	1.6	1.5	9.0	10.5	8.3	10.2
Std devn	5.64	6.37	7.79	8.53	1.32	1.61	3.54	2.88	4.66	3.93
t-value	−4.23		−0.69		0.43		−1.82		−3.09	
2-tail sig.	0.001		0.502		0.673		0.093		0.009	

Table 1. Change in species composition of sandplain heathland, in the absence of fire—Big Desert, Wyperfeld National Park. [A]A unique numerical identifier, assigned as part of the Flora Information System (Department of Natural Resources and the Environment, Victoria). [B]Some rarely-recorded growth forms have not been presented here.

Quadrat identifier[A]	Total spp. number[B] 1978	1992	Annual species 1978	1992	Serotinous shrubs 1978	1992	Perennial herbs 1978	1992	Non-serotinous shrubs 1978	1992	Dominance
A03037	20	31	9	7	0	1	5	14	5	8	*Leptospermum*
A03038	30	43	23	17	1	1	4	11	2	14	*Callitris verrucosa*
A03039	24	35	13	10	0	1	5	14	5	8	*Triodia*
A03040	30	33	14	8	0	2	7	12	6	8	*Kunzea pomifera*
A03041	17	29	8	6	0	1	4	10	3	11	*Leptospermum*
A03042	29	35	16	11	0	2	6	12	6	9	*Kunzea pomifera*
A03043	33	37	20	17	0	0	7	10	6	9	*Callitris gracilis*

t-test results

	Total spp. number 1978	1992	Annual species 1978	1992	Serotinous shrubs 1978	1992	Perennial herbs 1978	1992	Non-serotinous shrubs 1978	1992
Mean	26.1	34.7	14.7	10.9	0.1	1.1	5.43	11.9	4.71	9.57
Std devn	5.93	4.54	5.47	4.53	0.38	0.69	1.27	1.68	1.60	2.23
t-value	−5.51		5.76		−3.24		−7.91		−3.46	
2-tail sig.	0.002		0.001		0.018		0.000		0.013	

Table 2. Change in species composition of sandplain heathland, in the absence of fire—Wyperfeld National Park [A]A unique numerical identifier, assigned as part of the Flora Information System (Department of Natural Resources and the Environment, Victoria). [B]Some rarely-recorded growth forms have not been presented here.

These quadrats were typical sandplain heathland in 1978 (eg. dominated by *Banksia ornata*, *Casuarina* spp. and *Leptospermum* spp.). In spite of the absence of fire for the intervening 14 years, species not present in the quadrats in 1978 established and grew. The increase in species number was not due to an increase in the annuals nor the dominant serotinous shrubs. The increase was due to establishment and growth of a number of subordinate woody shrubs with non-serotinous fruits (both seed regenerators and root resprouters), including species of *Astroloma*, *Baeckea*, *Calytrix*, *Cryptandra*, *Hibbertia*, *Leucopogon* and *Spyridium*. How have these species managed to regenerate into mature heathland lacking the regeneration opportunities created by fire?

There was a severe frost in this part of Wyperfeld in 1982. Three successive nights of less than –11°C were recorded, with individual records reaching as low as –13°C (O'Brien 1989). One dramatic effect of this frost was to kill most (>90%) of the dominant *Banksia ornata* of the heathlands, within a few days of the frost event. Regeneration of *B. ornata* is abundant after fires, as the serotinous cones release much seed (Gill 1976; Gill & McMahon 1986). However, after the frost, the follicles of the banksias opened gradually over many years (if at all) and very few *B. ornata* seedlings managed to re-establish (O'Brien 1989; Cheal 1997). The resultant 'gaps' in the community enabled other (subordinate) shrubs to establish, particularly those without a seed reserve requiring some cue deriving from fire to break dormancy and initiate germination. Thus species number increased as the vegetation aged further, post-fire and post-frost.

The extraordinary frosts of 1982 mimicked the effects of fire in some ways (death of many dominants). However, this frost did not mimic fires in other ways. For instance, species other than *B. ornata* survived the event, there was no 'ash bed' effect of increased availability of limiting nutrients and there was no coordinated, mass seed release from the largely-dead *B. ornata*. This unusual event has enabled a regeneration response due to any generalised disturbance (in this case, frost) to be partially disentangled from a regeneration response due to the specific disturbance of fire. Serotiny is a strategy that appears to particularly suit regeneration of heathland species after fires. Other species may respond to disturbance *per se*, whether by fire or some other means. Fires are a dramatic 'disturbance' in heathlands, but other disturbances also occur. These disturbances may be very localised (eg. death of an individual shrub due to disease), but nevertheless provide regeneration opportunities.

In this study, the successfully regenerating subshrubs all have either small barely-woody capsules or fleshy fruit. Such structures are not well-adapted for seed survival during fire (Westoby et al. 1991; Judd 1994; French & Westoby 1996). Some may be myrmecochorous (ie. ant-dispersed), eg. species of *Boronia*, *Comesperma*, *Cryptandra*, *Eriostemon*, *Hybanthus*, *Phebalium* and *Spyridium* (Berg 1975; Westoby et al. 1991; French & Westoby 1996). Ant dispersal enables the otherwise dangerously-exposed seeds to be placed in fire-protected sites or dispersed to gaps within the community, enabling germination without fire cues. A few species are presumably vertebrate-dispersed, eg. *Astroloma* spp., *Billardiera cymosa*, *Cassytha* spp., *Einadia nutans*, *Exocarpos spartens* and *Kunzea pomifera* (French & Westoby 1996). Any component of vertebrate dispersal is a very uncertain strategy in fire-prone environments, as vertebrates usually deposit seeds in exposed situations, such as at the soil surface or elevated on shrubs (French & Westoby 1996). It is a curious strategy for species whose supposedly sole regeneration opportunities are immediately following fires. With the exception of *Kunzea pomifera*, the common small myrtaceous shrubs do not appear to be zoochorous. The capsules may be either weakly explosive or the seeds passively dispersed. Whichever strategy is adopted by *Baeckea* spp., *Calytrix* spp. and *Micromyrtus ciliata*, these fruit are also not well-adapted to withstand fires (Judd 1994). None of these common under-shrubs is notably serotinous. In addition, they do not appear to respond to fire-derived germination cues (Keith 1996), either from smoke or ash. The small woody shrubs are a common and consistent component of these heathlands and yet show few adaptations to a regime of relatively frequent fires.

Since Specht's seminal work of about 40 years ago (Specht & Rayson 1957; Specht et al. 1958), it has become a paradigm of heathland ecology that the principal and determinative regeneration events occur immediately after fires (Posamentier et al. 1981; Kruger 1983; Bell et al. 1984; Lamont 1992; Myerscough et al. 1995; Bradstock et al. 1997). Indeed, available models of heathland processes subscribe to this paradigm to such an extent that they assume regeneration occurs only after fires, eg. Gill & Groves 1981; Specht 1981; Kruger 1983; Bell et al. 1984; McMahon 1984; McFarland 1988; Offor 1990; Myerscough et al. 1995; Myerscough et al. 1996; Clarke et al. 1996. A few authors have referred to occasional seedling regeneration in undisturbed (= unburnt) heathlands, *viz.* Hnatiuk & Hopkins 1980; Bradstock & O'Connell 1988; Bradstock 1990; Enright et al. 1994. Such regeneration may be common enough to maintain an obligately seed regenerating serotinous shrub as a dominant, even without the opportunities for abundant seedling regeneration immediately after fires (Bradstock & O'Connell 1988; Bradstock 1990). Nevertheless, recent models still assume negligible recruitment without fire, eg. Keith & Bradstock (1994) and Keith (1996), perhaps because most work has centred on serotinous species or fire ephemerals, and other heathland components, such as the subordinate shrubs discussed above, have been substantially overlooked. It is tempting to suggest that serotiny, with its reliance on the opportunities presented post-fire, is clearly advantageous for long-lived shrubs (those likely to experience a fire well before senescence of individuals) but a poor strategy for shorter-lived shrubs with a low probability of being burnt before senescence.

Heathland in Wyperfeld appears to be an amalgam of vegetation guilds, *sensu* Lamont 1992, each with its own regeneration requirements and responses to disturbances, such as fire. The relative proportions of each guild present at a particular site are dependent on the local combination of features, particularly (but not solely) fire history. Fires are a critical determinant of vegetation composition and processes. But the stochastic nature of fires enables guilds and species with apparently conflicting requirements to coexist, including species for which fire is merely yet another disturbance or even detrimental. Individual species' abundances and dominance are dependent on the frequency and nature of such disturbances. The vegetation composition at a site and at one point in time is an unbalanced conglomeration of species (or guilds of species), some with conflicting habitat requirements. Thus species composition may change with time, with or without fire.

The species composition of sandplain heathlands in Wyperfeld will change in the continuing absence of fire. This change is not a unidirectional decline in species number (the now-classic decrease in species richness as heathland ages). Some components of the vegetation will increase in abundance and importance. Although this change may occur at a low rate, it is not negligible. With their obligately low growth rates, heathland species do not show rapid changes in the absence of fire. Nevertheless, on-going change is a feature of heathland growth. The composite nature of vegetation communities means that some species will decrease as these communities age and others will increase, including establishment from seed.

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REFERENCES

Bell, D. T., Hopkins, A. J. M. & Pate, J. S., 1984. Fire in the Kwongan. In *Kwongan Plant Life of the Sandplain*, J. S. Pate & J. S. Beard, eds, University of Western Australia Press, Nedlands. 178–204.

Berg, R. Y., 1975. Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Botany* 23: 475–508.

Bolton, 1915. *Feature Survey of the Country along the Outlet Creek, north of the Parish of Nypo and Lake Albacutya towards Pine Plains. Counties of Karkarooc and Weeah.* Department of Lands and Survey, Melbourne.

Bradstock, R. A., 1990. Demography of woody plants in relation to fire: *Banksia serrata* Lf. and *Isopogon anemonifolius* (Salisb.) Knight. *Australian Journal of Ecology* 15: 117–132.

Bradstock, R. A. & Myerscough, P. J., 1988. The survival and population response to frequent fires of two woody resprouters *Banksia serrata* and *Isopogon anemonifolius. Australian Journal of Botany* 36: 415–431.

Bradstock, R. A. & O'Connell, M. A., 1988. Demography of woody plants in relation to fire: *Banksia ericifolia* Lf. and *Petrophile pulchella* (Schrad.) R. Br. *Australian Journal of Ecology* 13: 505–518.

Bradstock, R A., Tozer, M. G. & Keith, D. A., 1997. Effects of high frequency fire on floristic composition and abundance in a fire-prone heathland near Sydney. *Australian Journal of Botany* 45(4): 641–655.

Cheal, D. C., 1997. Survival of desert banksia *Banksia ornata* seed in detached cones. *Victorian Naturalist* 114(4): 190–191.

Cheal, D. C. & Parkes, D. M., 1989. Mallee vegetation in Victoria. In *Mediterranean Landscapes in Australia Mallee Ecosystems and their Management*, J. C. Noble & R. A. Bradstock, eds, CSIRO, Melbourne, 125–140.

Cheal, P., Day, J. & Meredith, C. W., 1979. *Fire in the National Parks of North-west Victoria.* Australian National Parks & Wildlife Service, Canberra.

Clarke, P. J., Myerscough, P. J. & Skelton, N. J., 1996. Plant coexistence in coastal heaths: Between- and within-habitat effects of competition, disturbance and predation in the post-fire environment. *Australian Journal of Ecology* 21(1): 55–63.

Enright, N. J., Miller, B. P. & Crawford, A., 1994. Environmental correlates of vegetation patterns and species richness in the northern Grampians, Victoria. *Australian Journal of Ecology* 19(2): 159–168.

French, K. & Westoby, M., 1996. Vertebrate-dispersed species in a fire-prone environment. *Australian Journal of Ecology* 21(4): 379–385.

Frood, D., 1979. *Dynamics of a post-1951 Fire in Heathland, Tidal Overlook, Wilsons Promontory, Victoria*. BSc(Hons) Thesis, School of Botany, University of Melbourne.

George, A. S., Hopkins, A. J. M. & Marchant, M. G., 1979. The heathlands of Western Australia. In *Heathlands and Related Shrublands of the World A. Descriptive Studies*, R. L. Specht, ed., Elsevier Scientific Publishing, Amsterdam, 211–229.

Gill, A. M., 1975. Fire and the Australian flora: A review. *Australian Forestry* 38(1): 4–25.

Gill, A. M., 1976. Fire and the opening of *Banksia ornata* follicles. *Australian Journal of Botany* 24(3): 329–335.

Gill, A. M. & Groves, R. H., 1981. Fire regimes in heathlands and their plant ecological effects. In *Ecosystems of the World 9B Heathlands and Related Shrublands Analytical Studies*, R. L. Specht, ed., Elsevier Scientific, New York, 61–84.

Gill, A. M. & McMahon, A., 1986. A post-fire chronosequence of cone, follicle and seed production in *Banksia ornata*. *Australian Journal of Botany* 34: 425–433.

Groves, R. H., 1983. Nutrient cycling in Australian heath and South African fynbos. In *Mediterranean-Type Ecosystems The Role of Nutrients*, F. J. Kruger, D. T. Mitchell, & J. U. M. Jarvis, eds, Springer-Verlag, Berlin, 179–191.

Groves, R. H. & Specht, R. L., 1981. Seral considerations in heathlands. In *Vegetation Classification in Australia*, A. N. Gillison & D. J. Anderson, eds, Australian National University Press, Canberra, 78–85.

Handreck, K. A., 1997. Phosphorus requirements of Australian native plants. *Australian Journal of Soil Research* 35(2): 241–289.

Hazard, J. & Parsons, R. F., 1977. Size-class analysis of coastal scrub and woodland, Western Port, southern Australia. *Australian Journal of Ecology* 2: 187–197.

Hilbert, D. W. & Larigauderie, A., 1990. The concept of stand senescence in chaparral and other mediterranean type ecosystems. *Acta Oecologica* 11(2): 181–190.

Hnatiuk, R. J. & Hopkins, A. J. M., 1980. Western Australian species-rich kwongan (sclerophyllous shrubland) affected by drought. *Australian Journal of Botany* 28: 573–585.

Hobbs, R. J. & Atkins, L., 1990. Fire-related dynamics of a *Banksia* woodland in south-western Western Australia. *Australian Journal of Botany* 38: 97–110.

Hwang, Y. H., 1992. The Casuarinaceae: *Allocasuarina* is unsupported. *Australian Systematic Botany Society Newsletter* 70: 16–19.

Johnson, L. A. S., 1982. Notes on Casuarinaceae II. *Journal of the Adelaide Botanic Gardens* 6(1): 73–87.

Judd, T. S., 1994. Do small myrtaceous seed-capsules display specialised insulating characteristics which protect seed during fire? *Annals of Botany* 73: 33–38.

Keeley, J. E., 1986. Resilience of mediterranean shrub communities to fire. In *Resilience in Mediterranean-type Ecosystems—Tasks for Vegetation Science 16*, B. Dell, A. J. M. Hopkins & B. B. Lamont, eds, Dr W. Junk, Dordrecht, 95–112.

Keith, D., 1996. Fire-driven extinction of plant populations: a synthesis of theory and review of evidence from Australian vegetation. *Proceedings of the Linnean Society of New South Wales* 116: 37–78.

Keith, D. A. & Bradstock, R. A., 1994. Fire and competition in Australian heath: a conceptual model and field investigations. *Journal of Vegetation Science* 5: 347–354.

Kruger, F. J., 1983. Plant community diversity and dynamics in relation to fire. In *Mediterranean-Type Ecosystems The Role of Nutrients*, F. J. Kruger, D. T. Mitchell & J. U. M. Jarvis, eds, Springer-Verlag, Berlin, 446–472.

Lamont, B. B., 1992. Functional interactions within plants—the contribution of keystone and other species to biological diversity. In *Biodiversity of Mediterranean Ecosystems in Australia*, R. J. Hobbs, ed., Surrey Beatty & Sons, Chipping Norton, 95–127.

McFarland, D. C., 1988. Fire and the vegetation composition and structure of subtropical heathlands in south-eastern Queensland. *Australian Journal of Botany* 36: 533–546.

McMahon, A., 1977. *The Effect of Fire on Heath Floristics in the Little Desert National Park, Victoria*. Botany Department, LaTrobe University, Bundoora.

McMahon, A., 1984. The effects of fire regime components on heathlands in the Little Desert, N.W. Victoria, Australia. *MEDECOS IV 4th International Conference on Mediterranean Ecosystems*. University of Western Australia, Perth.

Myerscough, P. J., Clarke, P. J. & Skelton, N. J., 1995. Plant coexistence in coastal heaths: Floristic patterns and species attributes. *Australian Journal of Ecology* 20(4): 482–493.

Myerscough, P. J., Clarke, P. J. & Skelton, N. J., 1996. Plant coexistence in coastal heaths: Habitat segregation in the post-fire environment. *Australian Journal of Ecology* 21(1): 47–54.

O'Brien, T. P., 1989. The impact of severe frost. In *Mediterranean Landscapes in Australia Mallee Ecosystems and Their Management*, J. C. Noble & R. A. Bradstock, eds, CSIRO, Melbourne, 181–188.

O'Connell, A. M., Grove, T. S. & Dimmock, G. M., 1978. Nutrients in the litter on jarrah forest soils. *Australian Journal of Ecology* 3: 253–260.

Offor, T., 1990. What future for the sandy heaths of Wilson's Promontory. *Victorian Naturalist* 107(4): 120–123.

Posamentier, H. G., Clark, S. S., Hain, D. L. & Recher, H. F., 1981. Succession following wildfire in coastal heathland (Nadgee Nature Reserve N.S.W.). *Australian Journal of Ecology* 6: 165–175.

Rundel, P. W., 1983. Impact of fire on nutrient cycles in mediterranean-type ecosystems with reference to chaparral. In *Mediterranean-Type Ecosystems The Role of Nutrients*, F. J. Kruger, D. T. Mitchell & J. U. M. Jarvis, eds. Springer-Verlag, Berlin, 192–207.

Russell, R. P. & Parsons, R. F., 1978. Effects of time since fire on heath floristics at Wilson's Promontory, southern Australia. *Australian Journal of Botany* 26: 53–61.

Specht, R. L., 1981. Responses to fire of heathlands. In *Fire and the Australian Biota*, A. M. Gill, R. H. Groves & I. R. Noble, eds. Australian Academy of Science, Canberra, 395–416.

Specht, R. L. & Rayson, P., 1957. Dark Island heath (Ninety-Mile Plain, South Australia) I. Definition of the ecosystem. *Australian Journal of Botany* 5(1): 52–85.

Specht, R. L., Rayson, P. & Jackman, M. E., 1958. Dark Island heath (Ninety-Mile Plain, South Australia) VI. Pyric succession: changes in composition, coverage, dry weight and mineral nutrient status. *Australian Journal of Botany* 6(1): 59–88.

Walker, J. & Tunstall, B. R., 1981. *Field Estimation of Foliage Cover in Australian Woody Vegetation*. CSIRO, Division of Land Use Research, Canberra.

Walsh, N. G. & Entwisle, T. J., 1994. *Flora of Victoria Volume 2 Ferns and Allied Plants, Conifers and Monocotyledons*. Inkata Press, Melbourne.

Walsh, N. G. & Entwisle, T. J., 1996. *Flora of Victoria Volume 3 Dicotyledons Winteraceae to Myrtaceae*. Inkata Press, Melbourne.

Walsh, N. G. & Entwisle, T. J., 1999. *Flora of Victoria Volume 4 Dicotyledons Cornaceae to Asteraceae*. Inkata Press, Melbourne.

Wark, M. C., White, D. M., Robertson, D. J. & Marriott, P., 1987. Regeneration of heath and heath woodland in the north-eastern Otway Ranges following the wildfire of February 1983. *Proceedings of the Royal Society of Victoria* 99(2): 51–88.

Westoby, M., French, K., Hughes, L., Rice, B. & Rodgerson, L., 1991. Why do more plant species use ants for dispersal in infertile compared with fertile soils? *Australian Journal of Ecology* 16: 445–455.

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